SOCIALITY IN HARRIS'S HAWKS REVISITED: PATTERNS OF REPRODUCTIVE OUTPUT AND DELAYED DISPERSAL

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In the lower Rio Grande Valley of south Texas, more than half the nesting groups of Harris's hawks (*Parabuteo unicinctus*) include at least one auxiliary group member in addition to a breeding pair. To provide further insight into cooperatively breeding raptors, I evaluated sociality in Harris's hawks through the dual benefits framework. I explored the formation, structure, and stability of cooperative group formation across a spatially variable study area, which includes high levels of urbanization and development as well as remote, undisturbed native habitats with low anthropogenic impact. I used color banding, regular censuses of active territories, and a microsatellite relatedness analysis to examine patterns of sociality, including delayed dispersal, the effect of auxiliary group members on reproductive output, parentage of broods, and the relatedness of auxiliaries compared to the nestlings in their territories. I confirmed cooperative polygamy with genetic techniques for the first time in Harris's hawks and found 58% of juvenile hawks delayed dispersal for at least 6 mo. Using the dual benefits framework, I found social associations that formed through delayed dispersal followed predictions for resource-defense benefits, but sociality among mature non-related hawks more closely followed predictions associated with collective action benefits, specifically reproductive output was significantly reduced in undeveloped habitats, presumably due to a less predictable prey-base.

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PATTERNS OF REPRODUCTIVE OUTPUT AND DELAYED DISPERSAL

Introduction

Cooperatively breeding animals, in which some individuals reduce or forgo independent reproduction to help raise offspring that are not their own, are found across virtually every habitat, climate, and continent with the exception of Antarctica (Jetz and Rubenstein 2011, Dieter and Clutton-Brock 2017). How these cooperative dynamics evolve under natural selection pressure is central to understanding the evolution of sociality, but despite intense research focus (e.g., Cockburn 1998, 2006; Bergmüller et al. 2007, Hughes et al. 2008, Hatchwell 2009, Cornwallis et al. 2010, Nonacs and Hager 2011) the ultimate factors that promote sociality and cooperative breeding are unclear. The first hypothesis that attempted to explain cooperative breeding with wide support was Hamilton's Rule, or Inclusive Fitness Theory. It posits that helpers could balance the costs of foregoing reproduction by obtaining indirect fitness benefits when they help raise relatives (Hamilton 1964). Hamilton's Rule has been supported by many studies providing empirical evidence that cooperation is more common among related individuals (e.g., Browning et al. 2012, Lukas and Clutton-Brock 2012a, Hatchwell et al. 2014, Green et al. 2016), but it does not predict what ecological conditions favor cooperation (Nowak et al. 2010, Birch 2014). Similarly, it offers little explanation for non-kin cooperation, which may be more common than previously thought as more studies have explored parentage analyses using genetic methods (Riehl 2013).

With data on vertebrate life history traits, phylogenetic information, and habitat quality, a number of comparative studies of cooperative breeding have produced contradictory results (Kimball et al. 2003, Jetz and Rubenstein 2011, Lukas and Clutton-Brock 2012b, Downing et al.

2015, Dieter and Clutton-Brock 2017). Evidence suggests that sociality can occur in both stable (Gonzalez et al. 2013) and productive environments (Malan 2004), as well as harsh (Shen et al. 2016) and fluctuating ones (Rubenstein and Lovette 2007). This paradox between variation in environmental quality and the occurrence of cooperative breeding highlights the behavioral complexity of sociality and has given rise to more holistic frameworks for explaining cooperation and its evolutionary trajectory. For example, Griesser et al. (2017) described a two-step process for the transition from social monogamy to cooperative breeding in birds. They found a strong association between the initial formation of family groups by delayed dispersal of offspring was more likely in productive and seasonal environments where the costs of prolonged parent-offspring interactions are reduced. However, the subsequent evolution of cooperative breeding was more likely favored in harsh or fluctuating environments where helpers may buffer against reproductive failure in unfavorable conditions. Increasingly unstable habitats favored cooperative breeding in species that had already formed family-groups via delayed dispersal (Griesser et al. 2017). This novel framework based on over 3,000 bird species demonstrated the value of integrating historical evolutionary context and qualitative habitat variation into our understanding of complex adaptations like cooperative breeding.

Similarly, Shen et al. (2017) argued that many of the previous efforts describing cooperative breeding focused on the cost or benefit to the helper (Hamilton 1964, Emlen 1983, Stacey and Ligon 1991), while largely ignoring the potential for group formation conflicts between the existing group members (insiders) and the potential joiner (outsider). The resolution of insider-outsider conflicts, which occur even among highly-related individuals (Giraldeau and Caraco 1993), have predictable impacts on group formation, optimum group

size, kin structure, and group stability. Thus, these factors should be considered when developing a predictive framework for the evolution of sociality. Shen (2017) proposed the dual benefits framework to consider the per capita benefits of cooperation, while also incorporating the interests of established group members and potential joiners (i.e., insider-outsider conflicts). The first cooperative benefit type is *resource defense benefits* (RD), which increases fitness for those with access to group-defended critical resources and available resources decrease per capita as group size increases. RD benefits are more likely to develop when dispersing becomes more costly because of a shortage of either territories or mates for breeding opportunities (Wong 2010, Kingma et al. 2016) as originally proposed by the ecological constraints hypothesis (Emlen 1983). The second type of cooperative benefits are *collective action benefits* (CA) and are often the direct result of social cooperation among group members that cannot be obtained in solitary life. CA benefits will increase the per capita fitness of all group members as group size increases until optimum group size is reached, a relationship previously explained by the group augmentation hypothesis (Kingma et al. 2014). Although neither proposed benefit is mutually exclusive, in general, sociality that forms through CA benefits is influenced by temporal variation and RD-cooperation is shaped by spatial variation (Lin et al. 2019).

RD benefits are likely to be important for individuals in environments with high intraspecies competition and are most influential for group formation in territorial species with low mortality (Arnold and Owens 1998). In such cases, where competition for resource access (e.g., population density) is high (Komdeur 1992), groups are favored in stable, productive habitats with heterogenous quality (McNamara and Dall 2011). Group formation increases

fitness for an individual by providing access to resources they would otherwise be excluded from, such as those from high-quality territories, but increased group size negatively impacts the per capita available resources (Emlen 1983, Faaborg and Bednarz 1990, Koenig et al. 1992, Komdeur 1992). This typically results in kin-groups that form via delayed dispersal (Drobniak et al. 2015) and have low stability because the departure of offspring to obtain an independent breeding opportunity is beneficial for all group members (Emlen 1995). For example, Komdeur (1992) experimentally manipulated the number of available territories for Seychelles Warblers (*Acrocephalus sechellensis*), noting that more offspring delayed dispersal and became helpers when the number of available breeding territories were reduced. In Western Bluebirds (*Sialia mexicana*), reductions in valuable territorial resources (i.e., mistletoe) negatively influenced delayed dispersal, which linked access to critical resources to kinship sociality, but RD benefits can also favor non-kin cooperation. For example, unrelated nest attendants in Superb Fairywrens (*Malurus cyaneus*) help as payment to remain a member of the group, granting them access to a higher quality territory (Dunn et al. 1995). Galápagos hawks (*Buteo galapagoensis*) can also form cooperative polyandrous groups because several adult males are more successful defending a suitable nesting territory than solitary males, and subsequently share access to copulations with the breeding female (Faaborg et al. 1995).

CA benefits are the result of social cooperation and could include foraging advantages (Malan 2004, Hayward et al. 2006), increased offspring provisioning (Dunn et al. 1995, Bolopo et al. 2019), or predation detection and defense (Dawson and Mannan 1991a, Malan and Jenkins 1996). Obligate cooperative breeders provide an extreme example of when CA benefits become critical to survival or reproduction. This is seen in Chestnut-crowned Babblers

(*Pomatostomus ruficep*), in which breeding without supplemental provisioning from helpers is rarely successful (Russell 2016). Social groups that are formed or stabilized by CA benefits likely emerge as an adaptive response to ecological challenges, particularly fluctuating environments (Shen et al. 2017, Lin et al. 2019). Taiwan Yuhinas (*Yuhina brunneiceps*) are monogamous joint-nesters who cooperate with largely unrelated individuals to buffer against adverse breeding conditions (Shen et al. 2016). This suggests CA-cooperation is favored when environmental uncertainty drives temporal variation in selective pressures and allows cooperative groups to increase their performance during difficult seasons or in challenging environments (Gowaty 1981, Pusey and Packer 1994, Rubenstein and Lovette 2007, Jetz and Rubenstein 2011).

While comparative work has shown that most cooperatively breeding groups of birds are a nesting pair with retained offspring that function as non-breeding helpers (Hatchwell 2009, Drobniak et al. 2015), more complex arraignments of cooperation that include non-relatives are common in some lineages, such as in Accipitriformes and Falconiformes, or diurnal raptors (Kimball et al. 2003). Pale Chanting Goshawks (*Melierax canorus*), who occupy arid unpredictable habitats, form cooperatively breeding groups that were more likely to raise second clutches successfully (Malan and Jenkins 1996) and had less nest predation than monogamous pairs (Malan 1997). Diurnal raptors who adopt cooperative breeding strategies appear strongly associated with environmental instability, and typically form groups independent of or in addition to delayed dispersal (Kimball et al. 2003). African Pygmy Falcons (*Polihierax semitorquatus*), whose habitat overlaps with Pale Chanting Goshawks in South Africa, form social groups that include both kin and non-kin helpers at nearly half of nests, and the presence of helpers has been shown to improve the body condition of the nestlings (Bolopo

et al. 2019). CA benefits, which are understudied in empirical studies compared to RD benefits, could be vital to the reproductive success of raptors in challenging or complex habitats (Coulson and Coulson 2013).

Here, I use the Harris's hawk (*Parabuteo unicinctus*), a desert-dwelling raptor that adopts multiple breeding strategies from solitary pairs to cooperatively breeding groups (Dwyer and Bednarz 2020), to examine group formation, structure, stability, and reproductive performance using the dual benefits framework. While few cooperatively breeding raptors have received as much behavioral research focus as the Harris's hawk (e.g., Bednarz 1987, Bednarz and Hayden 1991, Dawson and Mannan 1991a, Clark 2017 and references therein), the factors that promote cooperative group formation, structure, and stability remain unclear across the species' geographical range.

In the southwestern U.S., Harris's hawks form facultative cooperative groups to breed and hunt (Dwyer and Bednarz 2020), and have been observed adopting many forms of complex reproductive strategies along a continuum with solitary breeding pairs at one extreme and (presumed) cooperative polygamy at the other (Mader 1975, Bednarz 1987, Dawson and Mannan 1991a, Clark 2017). In Arizona, for example, auxiliary adults at active nests assist with provisioning the breeding pair's offspring through solo and more commonly as cooperative hunts (Dawson and Mannan 1991a), suggesting group hunting may play a role in provisioning offspring as well as sustaining adult group members. Extra hawks associated with nests included both delayed dispersing offspring and adult auxiliary males who were observed copulating with the breeding female, indicating Harris's hawks could engage in cooperative polyandry (Mader 1975, Dawson and Mannan 1991a). It is not known, however, if those

copulations resulted in extra-pair offspring. In New Mexico, offspring often delayed dispersal to remain with their natal nest for up to 3 yr (Bednarz 1987), despite 12-15% of suitable breeding territories remaining unoccupied during the breeding season. Breeding pairs had more successful nests, but groups were more likely to attempt to raise a second brood (Bednarz 1987), suggesting that sociality among mature hawks was not associated with any perennial feature of the nesting territories, but as an adaptive response to temporal variation in habitat quality.

Preliminary observations of Harris's hawks in Texas reported they were predominately monogamous (Griffin 1976, Brannon 1980), suggesting there could be a longitudinal gradient of increasing sociality in Harris's hawks with Arizona showing the most complex forms of cooperative group structure and Texas hawks adopting mostly monogamous strategies (Dawson and Mannan 1991). Recent field research in south Texas, however, showed nearly half of nesting attempts (46%) were made by groups of more than two adult-plumaged hawks and less than 10% of social groups included juvenile auxiliaries during the primary breeding season (Clark 2017). Opportunistic observations revealed that at least occasionally adult auxiliaries provisioned chicks and mated with dominant breeders within their group (Clark pers comms.), but lack of marked birds prevented differentiation between hawks of the same sex and no other research has been published on this population.

Identifying how social groups form, interact, and vary is fundamental to understanding the evolution of cooperative breeding. Although most avian helpers are retained offspring from previous broods (Hatchwell 2009), unique species like the Harris's hawk, which form cooperative associations among both kin and non-kin individuals (Dwyer and Bednarz 2020),

can clarify how various environmental conditions and auxiliary demographics may impact group formation, structure, and stability. I suggest that there are key differences in the factors that shape cooperation between breeding hawks and auxiliaries, which are dependent upon a variety of complex and non-mutually exclusive influences, that may be best explained using the dual benefits framework (Shen et al. 2017). To examine the social dynamics of Harris's hawks in south Texas, I captured, marked, and blood sampled as many individual hawks and nests as possible. Meanwhile, I employed a regular census and resighting effort to document group membership, recruitment, stability, and patterns of delayed dispersal. Further, a microsatellite DNA analysis was used to estimate pairwise relatedness among broods and between all sampled group members to assess parentage and kin structure within sampled breeding territories.

Methods

Study Area

My study focuses on active Harris's hawk territories in Cameron, Hidalgo, and Willacy Counties of southern Texas. The area is often referred to as the lower Rio Grande Valley and is sub-tropical receiving an average 65 cm of precipitation annually. Major urban centers include Brownsville, Harlingen, McAllen, and their surrounding development; the human population sizes are 182,000, 142,000, and 65,000 respectively (U.S. Census Bureau 2019). Most nesting activities were documented during April through June when the average daytime temperatures were between 24-35°C. I recorded incubation beginning in mid-March through October and I documented nestlings fledging during every month except January and February. Rainfall was infrequent during the primary breeding season (April - June) and in June of 2018, substantial

flooding occurred when the study area received twice the average monthly rainfall in less than 2 days ending drought conditions that began mid-2016 (NIDIS 2021).

Harris's hawks maintain but do not aggressively defend territories against conspecifics (Bednarz 1987, Dawson and Mannan 1991b) and are nonmigratory (Dwyer and Bednarz 2020), therefore I use the word territory to refer to the nesting and foraging range used by the breeding pair and auxiliaries (when present), which was most commonly centralized around the active or most-recently used nest site. Harris's hawks selected territories in diverse habitats across the study site including both Laguna Atascosa National Wildlife Refuge (LANWR) and Lower Rio Grande Valley National Wildlife Refuge (LRGVNWR). The refuge habitats are characterized by Tamaulipan brushland (Jahrsdoerfer and Leslie 1988), which is dominated by Spanish dagger yucca (*Yucca treculeana*), Texas ebony (*Ebenopsis ebano*) and honey mesquite trees (*Prosopis glandulosa*). Spanish dagger yucca was their preferred nesting substrate on both refuges. Harris's hawks frequently nested in more developed habitats such as cemeteries, recreational vehicle parks, agricultural areas, urban parks, wildlife sanctuaries, and in a few cases directly in urban environments where they nested between billboards, on powerlines, and in trees alongside roadways. As reported with other urban Harris's hawks (Boal and Dwyer 2018), they are well acclimatized to human activity across the study area making them relatively easy research subjects compared to other raptor species (Bednarz 2007).

Census: Reproductive Output and Delayed Dispersal

Between January 2018 – June 2020, I monitored 65 Harris's hawk territories for nesting activity, such as copulations or nest building. Most territories were identified in 2014-2015 during a previous study (Clark 2017), or by incidentally observing groups within the study area.

At least 10 attempts were reported as the result of a citizen science campaign to locate active Harris's hawks nests. The outreach effort included regular posting in wildlife and birding social media groups for the lower Rio Grande Valley, coordinating citizen teams to monitor selected local territories, and information signage at wildlife refuge visitor centers to engage local avian professionals and hobbyists within the study area.

I monitored active nests from the time they were discovered by visiting the nest weekly until the nestlings were approximately 3 wk old, at which time I sampled the nest. To access nests, I used standard arborist climbing techniques (Anderson et al. 2015) or an extension ladder. I recorded 96 fledglings from 48 nests and sampled 74 nestlings from 39 nests. Nestlings were only designated as fledged if they were observed after leaving the nest, consistent with previous studies (Bednarz 1987). There were 41 unique territories where at least one breeding attempt was made and 61 total nesting attempts recorded (Figure 1).

To identify individual hawks, adult and free-flying juveniles were targeted for capture during the winter and spring seasons from 2018-2020. I used Bal-chatri traps (Berger and Mueller 1959) with lures of domestic mice (*Mus musculus*), domestic gerbils (*Meriones unguiculatus*), Eurasian-collared Doves (*Streptopelia decaocto*), or House Sparrows (*Passer domesticus*) to trap individuals along roadways, which were relatively common throughout the study area, within territories. When one or more hawk(s) were sighted, one to three Bal-Chatri traps (Berger and Mueller 1959) were placed beside the road or under a habitually used perch. Traps were monitored continuously until a hawk was captured, or until the target hawk lost interest in the trap. Hawks were handled for less than 20 min and processing included banding, standard morphometric measurements, documenting molt and plumage irregularities, and

blood sampling. All sampled hawks, including nestlings, received a U.S. Geological Survey band and a uniquely coded anodized color band with a 2-digit code (ACRAFT Sign and Nameplate Co., Edmonton, Canada), which enabled in-field identification of individual group members.

I completed a tri-annual census of any territory where Harris's hawks attempted to nest to document the occurrence of delayed dispersal for at least 12 months post-fledging (March 2018 – June 2020). Based on the phenology of Harris's hawks (Dwyer and Bednarz 2020) and the time available for field work, I performed a seasonal census in Winter (December – January), Spring (March), and Summer (April – June). For each census, I visited monitored territories until I had five independent observations of each territory's occupants, or until I had made at least five visits to a territory with no signs of Harris's hawk activity. Once a territory member was sighted, I would observe the individual(s) for at least 30 min, documenting any noteworthy behavior, such as copulations, hunting attempts, vocalizations, nest building, prey transfers, or any other interactions among individuals. I documented the group membership of each territory, including age and sex of as many group members as possible.

To classify territories as urban or undeveloped, I extracted land cover data (Multi-Resolution Land Characteristics Consortium 2016) and chose a 977-m buffer radius around active nests as a proxy territory because a circle of this area approximates the known average home range size for Harris's hawks (Bednarz and Hayden 1991, Dwyer and Bednarz 2020). Urbanization, a measure of anthropogenic influence on habitat, was described using "urban" if the territory was within 1 km of an urban cluster with at least 2,500 people (U.S. Census Bureau 2010) or had more than 10% of the territory fall under the National Land Cover Database definition of "developed land" (Multi-Resolution Land Characteristics Consortium 2016). The

remaining territories were designated undeveloped, meaning 10% or less of the territory was developed and they were at least 1 km away from an urban cluster.

I used nearest neighbor distance (NND) as a measurement of conspecific density, and I reported it as the distance between the focal nest within a territory and the center (most recently active nest) of the closest occupied territory. NND was only included for the analysis of delayed dispersal.

Social-unit size was documented using the presence (groups) or absence (pairs) of adult-plumaged auxiliary group members in nesting territories. The presence of juvenile auxiliaries was recorded independently because the behavioral roles and cooperative investments differ between juvenile and mature auxiliaries (Bednarz 1987, Dawson and Mannan 1991a). To avoid over-estimating the occurrence of group-occupied territories due to the temporary presence of vagrant adult individuals, which were occasionally observed across the study area, I only designated breeding units as a group if more than two adult individuals were documented in a territory on at least two of the five territory observations during the censuses. Solitary breeding pairs were designated when no more than two adults were observed on any of the five territory observations for the seasonal census. There were 35 territories with sufficient census information to determine breeding unit size and social-unit size did not change in any territory between 2018 and 2019.

Most raptor species disperse from their natal territory less than 6 mo after hatching (Serrano 2018). Therefore, I designated a fledgling hawk as a “delayed disperser” if it remained associated with its natal group for 6 mo or longer after leaving the nest. To supplement my census observations of group membership and dispersal timing outside of my scheduled census

periods, I engaged my citizen science network with regular social media updates, signage at parks and refuges, educational outreach with local avian interest groups, and word-of-mouth with bird enthusiasts to connect with the wide-reaching birding community of south Texas. I accepted reports that included a photograph, to verify the band code, for inclusion in my group membership data. There were nine banded nestlings that disappeared with their parents shortly after fledging and were never relocated, therefore I excluded them from the analysis on delayed dispersal. I examined relationships with chi-square tests prior to model building (see below).

Generalized Linear Mixed Models

To investigate which biological, temporal, and spatial variables influence delayed dispersal and reproductive output, I used general linear mixed models (GLMM, R package lme4 v1.1.18.1; Bates et al. 2015). For all models, I used year as a random effect to control for territories sampled in 2018 and 2019. Prior to model construction continuous variables were checked for correlation ($r > 0.75$), categorical variable correlations were assessed using a χ^2 test ($p < 0.05$), and I checked for outliers with Cook's distance (Cook's $D > 1$) with none present. There was a significant association between social-unit size and urbanization ($\chi^2 = 4.4941$, $p = 0.03$), but each could influence delayed dispersal and reproductive output in different ways. Instead of excluding either variable, I opted to build two potential candidate model sets for each GLMM; one that included only social-unit size and another with only urbanization.

For the reproductive output models (ROM), I added territory as a random effect to control for multiple annual nesting attempts within territories. I used a poisson distribution to examine per-capita reproductive output (brood size, fledglings per nest) and annual fledglings

per territory as response variables. I constructed my ROM with predictor variables social-unit size (group/pair), auxiliary juveniles (yes/no), urbanization (urban/undeveloped), hatch month, and year.

In the natal philopatry, or delayed dispersal, models (NPM), I set individual breeding attempts ("nestID") as a nested random effect within the territory to account for territories and nests that had multiple nestlings sampled within or among years. I constructed my NPMs with response variables, occurrence of natal philopatry using a binomial distribution and duration of delayed dispersal (poisson distribution). Nestling sex, brood size, hatch day of the year, social-unit size (group/pair), auxiliary juveniles (yes/no), urbanization (urban/undeveloped), and NND were examined as potential fixed effect variables for inclusion in the natal philopatry GLMM.

In the first stage of model building, I evaluated all the biological and temporal variables, including all possible combinations of the variables excluding interactions, and selected the best model from this stage (lowest AIC_c) to move into the second stage analysis. Next, I evaluated habitat variables to determine that produced the model with the lowest AIC_c and from these I selected the stage two variables (Jara et al. 2020). The final model incorporated the best fit variables from each stage and was assessed for goodness of fit using χ^2 test to accept the model if $p > 0.05$. The explanatory variable(s) were assessed for importance by determining if their 95% CI included zero (Burnham and Anderson 2002).

Relatedness Analysis

Approximately 0.2 ml of blood was collected from the brachial vein of all nestlings and captured hawks and then stored in QueensLysis buffer at room temperature in the field, then at 4°C in the laboratory (Owen 2011). DNA was extracted from all samples using the DNeasy Blood

and Tissue Kit following manufacturer's protocols (Qiagen, Inc.), and extracted DNA was kept at -80°C to preserve the DNA for genetic analysis (see below).

I screened 16 microsatellite loci (B220, D107, D324, D234, D123, D220, D207, D223, D310, D122, D127, D235, D330, A312, A303, A317) previously described for Red-shouldered hawk (*Buteo lineatus*; Hull et al. 2008) for polymorphism in Harris's hawks. Only one of the loci did not amplify (D223) and an additional four were not polymorphic in Harris's hawks (D330, A312, A303, A317). Each individual was genotyped at the remaining 11 loci using polymerase chain reactions (PCR) in 10 µL volumes with 1 µL DNA (20-80ng) and various concentrations of forward fluorescently dye-labelled (Applied Biosystems Inc.), reverse primers (BioSource), $MgCl_2$, dNTP, and polymerase in volumes ranging from 0.05 to 0.15 µm as described elsewhere (Hull et al. 2008). Fluorescent primers (B220, D107, D324, D123, D220, D207, D223, D310) thermal cycling parameters were as follows: 94 °C for 2 min followed by 30 cycles of 94 °C for 30 s, 58 °C for 45 s and 72 °C for 45 s, and a final 30-min extension at 72 °C followed by 15 °C until further use (Hull et al. 2007). Primers with fluorescent labels added during PCR (D122, D127, D235) used thermal cycling parameters were as follows: 94 °C for 2 min followed by 30 cycles of 94 °C for 30 s, 58 °C for 45 s, 72 °C for 45 s, and a final 30-min extension at 72 °C followed by 15 °C (Blacket et al. 2012). I genotyped samples using an ABI 3130xl Genetic Analyzer (Applied BioSystems) and the program GeneMarker v.1.6 (SoftGenetics, LLC). All samples were genotyped at the 11 polymorphic microsatellite loci.

There were three microsatellite loci (D123, D107, D207) that showed signs of null alleles and were excluded from the analysis. Using the remaining eight microsatellite loci, I calculated pairwise genetic estimates of relatedness among all sampled individuals using

Wang's relatedness coefficient, r_w (Wang 2002) with the R package *related* (Pew et al. 2015) in R v.3.6.3 (R Core Team 2019). I performed simulation analyses to determine which of seven different methods for calculating relatedness with COANCESTRY was most appropriate given the characteristics of the generated microsatellite dataset (Csilléry et al. 2006, Taylor 2015). Data sets of 100 simulated pairs for four relatedness categories (parent–offspring [PO], full-sibling [FS], half-sibling [HS], and unrelated [UR]) were simulated, with allele frequencies calculated from the reference population allele frequencies. I then calculated relatedness using seven estimators and compared the observed relatedness estimates from simulations to those of the expected relatedness values (PO = 0.5, FS = 0.5, HS = 0.25, and UR = 0.0) by calculating the correlation coefficient in R. The Wang (2002) estimator was identified with the highest correlation coefficient (Pearson's r = 0.87) and used in subsequent analyses. Pairwise relatedness values were compared using their 95% confidence intervals that were calculated using bootstrapping over loci (1000 replicates). Accuracy of relatedness estimates between individuals can depend on many factors such as the level of polymorphism in the microsatellite loci and the number of microsatellite loci sampled (Csilléry et al. 2006). I had relatively large sampling variance for my pairwise relatedness estimates (CI r_w = 0.57 ± 0.18) for all sampled individuals, which is expected for microsatellite data (Johnson et al. 2021). I was therefore conservative in my designations of cooperative polygamy, kin or related auxiliary, and non-kin or unrelated auxiliary.

I sampled 37 broods that included at least two nestlings. If monogamy is assumed, individuals from the same nest should have full-sibship relationships (r_w ~ 0.5), whereas half-sibs could occur from either polyandry or polygyny (r_w ~ 0.25). I attempted to confirm half-sib

relationships for all nests using parent-offspring comparisons when available and by using diploid inheritance patterns to exclude full sibship based on the frequency of each allele between (presumed) siblings. Nests were designated as suspected monogamous if the mean r_w of the nestlings was > 0.5 and none of the nestlings had lower r_w CI > 0.20, or if available parental genotypes could help support monogamy.

To explore the relatedness of auxiliary group members to their group's offspring, I used the microsatellite analysis described above to obtain pairwise relatedness estimates among the 36 free-flying Harris's hawk group members I captured from territories with sampled nestlings or group members. I frequently observed unsampled hawks and was relatively successful, approximately one success per four attempts, at capturing juvenile hawks, but was unable to capture adult hawks at 55% (*n* = 19) of sampled territories due to trap aversion.

To eliminate breeding hawks from my analysis on auxiliaries, I examined every adult against the relatedness threshold, which I designated as an upper 95% CI of r_w > 0.45 and lower 95% CI of r_w > 0.01 on average compared to the nestlings or known breeders. For adults who met the threshold, I compared allele calls at each locus to determine if parenthood could be ruled out using diploid inheritance patterns. If an adult group member met the relatedness threshold and diploid inheritance patterns could not rule out parenthood, I examined the behavior of the potential breeder (frequency of chick feedings and prey deliveries) on nest cameras when available (Hagler and Gibbons unpub. data), used in-field observations of the individual (copulations, nest building, displacement of subordinate group members) during the tri-annual census of the population, and reexamined morphological measurements and physical observations from the individual's sample date (such as brood patch development in females).

In one case, an adult female met all the criteria for a primary breeder but was designated as an auxiliary because she did not have a brood patch despite being trapped while the nest was active.

I classified related auxiliaries as those with $r_w > 0.25$ and who met the relatedness threshold. Any group member who did not meet the relatedness threshold was then considered for non-kin designation. Individuals with a $r_w < 0.1$ an upper 95% CI of $r_w < 0.25$ were classified as unrelated or non-kin auxiliaries. Sampled group members who did not meet the criteria of either designation were marked as unknown and excluded from analysis ($n = 3$). I used Pearson's Chi-squared test with Yates' continuity correction ($p < 0.05$) in R v.3.6.3 (R Core Team 2019) to determine if there were differences in the number of kin and non-kin auxiliaries based on the demographic markers age and sex.

Results

Reproductive Output

I color banded 280 individual Harris's hawks across the study area from January 2018 – March 2020 (2018, $n = 114$; 2019, $n = 129$; 2020, $n = 37$). I marked 126 adults, 80 juveniles, and 74 nestlings, including 136 females and 144 males across all seasons of the study. I trapped significantly more ($\chi^2 = 19.575$, df = 1, $p = 0.00001$) juvenile-plumaged individuals ($n = 57$) following the 2019 breeding season compared to the post-2018 breeding season ($n = 13$) and the number of adults trapped decreased slightly from 36 individuals in 2018 to 27 individuals in 2019.

I monitored 41 nesting Harris's hawk territories located across the study area between January of 2018 – June 2020. There were 11 territories in which birds attempted to nest both

years, 9 territories with hawks that attempted to nest more than once during the same calendar year, and only one monitored territory that failed both years. Territories that had two successful nesting attempts in one year, or "second broods" (*n* = 5) were only observed in 2019. At six territories, I could not establish social-unit size (Table 1).

I documented 61 nest attempts that produced 96 fledglings from 48 successful nests (Table 1). There were 24 nesting attempts by breeding pairs, 21 attempts by cooperative adult group) and six nest attempts in territories that included juvenile auxiliaries (Table 1). The average brood size was 2.1 ± 0.8 nestlings and successful nests fledged an average of 2.0 ± 0.9 offspring (Table 2). Territorial breeding units made an average of 1.2 ± 0.5 nesting attempts annually and 75% of those attempts were successful and territories produced 1.7 ± 1.4 fledglings each year on average (Table 2).

There was reduced reproductive output in 2018 that was consistent across all measures of reproductive output (brood size 1.8 ± 0.6, mean fledglings per nest 1.7 ± 0.6, mean annual fledglings per territory 1.3 ± 0.6, successful nests *n* = 11, total fledglings *n* = 20) compared to 2019 (mean brood size 2.2 ± 0.9, mean fledglings per nest 2.1 ± 0.9, mean annual fledglings per territory 2.0 ± 1.5, successful nests *n* = 37, total fledglings *n* = 76), but none of these differences were statisticaly significant (Table 1 and 2).

There was no effect of social-unit size on reproductive success, but solitary pairs (*n* = 20) were significantly more likely to use urban territories (*n* = 15) than undeveloped ones (*n* = 5) and cooperative groups (*n* = 15) were documented more frequently in undeveloped habitats (*n* = 10) than breeding pairs (*n* = 5). Census observations of group membership found 80% of adult auxiliary group members were males (*n* = 12). The occurrence of sociality among mature

Harris's hawks in southern Texas was negatively correlated with habitat urbanization compared to breeding pairs ($\chi^2 = 4.4941$, df = 1, $p = 0.034$).

There was a significant effect on the per-capita reproductive output of nesting territories (mean annual fledglings per territory) in the urban habitats compared to the undeveloped habitat ($Z = 2.275$, df = 42, $p = 0.023$). Reproductive output was higher in urban territories (mean brood size: 2.3 ± 0.9, mean fledglings per nest: 2.2 ± 0.9, mean annual fledglings per territory: 2.1 ± 1.7, successful nests $n = 36$, total fledglings $n = 69$; Table 1 and 2) compared to undeveloped territories (brood size: 1.8 ± 0.7, fledglings per nest: 1.7 ± 0.7, annual fledglings per territory: 1.3 ± 0.9, successful nests = 25, total fledglings $n = 27$; Table 1 and 2).

Delayed Dispersal

Of the 65 Harris's hawk nestlings who were included in the natal philopatry analysis, 58% ($n = 38$) delayed dispersal for at least 6 mo post-fledgling. The average length of delayed dispersal (philopatry) was 4.6 mo and the median length of dispersal was 6 mo. Extended philopatry (delayed dispersal for longer than 12 mo) was documented for 8% ($n = 5$) of the sampled nestlings (Table S1). I observed four of the banded fledglings outside of their natal territories; two that were observed over 20 km from their nesting territory and were never resighted, one that was observed for two consecutive days with the adults in a territory 5 km away who returned to his natal group less than a week later, and one that joined another group 3.5 km away and was documented in that territory during two different seasonal censuses.

Delayed dispersal was recorded for 67% ($n = 24$) of nestlings whose group only had a breeding pair compared to the 48% ($n = 14$) of nestlings who delayed dispersal in group-occupied territories. Also, nestlings in group territories remained philopatric (mean = 4.0 mo)

for less time than those produced in pairs. (mean = 5.1 mo). None of the differences in delayed dispersal patterns between pair and group occupied territories were significant and group size was ultimately excluded as a predictive variable in the GLMM.

Nestlings in urban habitats dispersed significantly earlier than their non-urban counterparts using chi-square tests ($\chi^2 = 6.552$, df = 1, $p = 0.01$) and extended philopatry was never recorded in urban territories (Table S1). But urbanization was ultimately eliminated from inclusion during the model fitting stage and showed no statistical relationship with natal philopatry.

The occurrence of delayed dispersal was influenced by nestling sex and nearest neighbor distance (Figure 2; $Z = 2.046$, df = 59, $p = 0.041$) and the length of natal philopatry was influenced by nestling sex alone (Figure 3; $Z = 2.890$, df = 59, $p = 0.004$). Patterns of natal philopatry were male-biased and nearest neighbor distance negatively influenced the occurrence of delayed dispersal, although the pattern was border-line insignificant (Table 3).

Mixed Parentage

Mixed parentage was confirmed in 8% ($n = 3$) and monogamous breeding was suspected in 27% ($n = 10$) of the 37 sampled Harris's hawk broods with at least two nestlings (Table S2). At two mixed-parentage broods I used diploid inheritance patterns and allelic random assortment to confirm three parents and in the remaining brood the pairwise estimate was $r_w = -0.10 \pm 0.19$. At this territory, I observed extra-pair copulations three independent times between the adults in this territory. There were four additional broods where cooperative polygamy was suspected but could not be confirmed (Table S3). Mixed-parentage broods had an average

pairwise estimate of $r_w = 0.19$, confirmed monogamous broods nestling were on average $r_w = 0.66$ and suspected cooperative polygamy had an average $r_w = 0.35$ (Figure 4).

Auxiliary Relatedness

I sampled 23 auxiliary individuals at 14 Harris's hawk territories and 20 were successfully given relatedness (kin) designations (Table S4). Of those 20 with established kinships, there were 17 related (kin) auxiliaries, 3 unrelated (non-kin) auxiliaries, 15 juveniles, 5 adults, 9 females, and 11 males (Table 4). There were no differences in the relatedness of males compared to females ($\chi^2 = 1.14$, $p = 0.3$). Only adults were documented as non-kin auxiliary and kin auxiliaries were significantly more likely to be juveniles than adults ($\chi^2 = 6.41$, $p = 0.01$).

Discussion

Across south Texas, in 2018 I observed a depression in reproduction compared with previous years (Clark pers. comms.). I monitored approximately 100 historically active nesting Harris's hawk territories in the lower Rio Grande Valley that were previously studied by Clark (2017) and I documented only 16 nesting attempts with a total of 27 fledged nestlings. The following year in 2019, there were 380% more offspring fledged. The increase in reproductive output in 2019 compared to 2018 was consistent across all measures of reproductive output and significantly more juvenile plumaged individuals were trapped following the 2019 breeding season compared to the year before. The suspension of normal breeding activity across much of the study area in 2018 highlights the reproductive flexibility within Harris's hawk territories, sometimes referred to as a boom-or-bust reproductive pattern, which has been described for other Harris's hawk populations (Bednarz 2010, Coulson and Coulson 2013, Dwyer and Bednarz

2020). For species who occupy their territories year round, environmental uncertainty can strongly influence temporal variation in selective pressures, such as prey availability, which is expected to shape life history responses (Hayward et al. 2006, Jetz and Rubenstein 2011, Kettel et al. 2018). This suggests that similar to other diurnal raptor species, Harris's hawks occupy unpredictable habitats (Kimball et al. 2003) and modulate their reproduction, and defer reproductive efforts entirely in difficult seasons, and engage in multiple nesting attempts during abundant ones (Bednarz 2010).

Urban nesters were significantly more likely to be breeding pairs and reared significantly more fledglings on an annual basis compared to nest attempts in undeveloped habitats. This relationship suggests that undeveloped habitats may favor social associations among adult Harris's hawks independent of delayed dispersal. This pattern could be the result of variation in seasonal resource availability for urban territories compared to undeveloped habitats of south Texas. My results are consistent with urban-dwelling Harris's hawks in Arizona who bred mostly in solitary pairs, but raised more broods and produced more than twice as many fledglings annually as their Sonoran desert counterparts (Dawson and Mannan 1994). Territories with high anthropogenic influence could be shielded from unpredictable temporal variation in habitat quality related to drought or other climate extremes (Suri et al. 2017). Agriculture, landscaping, and other human-related activities may also create habitats that support stable and abundant prey communities (Kettel et al. 2018). High and stable prey abundance could increase independent breeding opportunities that may not be available to individuals in undeveloped habitats. Prey deliveries at nests for south Texas Harris's hawks showed that urban hawks delivered more avian prey items compared to undeveloped habitats where mostly

rodents were identified (Hagler and Gibbons unpub. data), suggesting there are notable differences in the prey communities exploited by urban hawks. These differences could explain the greater adult sociality in undeveloped habitats. The local prey community may require hawks to use cooperative hunting techniques more often to capture larger or more elusive prey (Bednarz 1988) or to increase overall hunting success in complex or challenging habitats (Stander 1991, Malan 1998, Coulson and Coulson 2013), as has been suggested for other cooperatively breeding populations of Harris's hawks.

Harris's hawks fledglings in the lower Rio Grande Valley commonly delayed dispersal to join social groups in their natal territories, compared to other raptor species who are reported to form cooperative groups with mostly adult individuals (Kimball et al. 2003). Despite high occurrence of delayed dispersal, relatively few individuals were observed in their natal territories during the following breeding season. All the juvenile auxiliaries I trapped in focal territories were related to the nestlings, which indicates they are likely offspring from previous broods that remained with their family group. More than half of the adult auxiliaries, however, were not related to any of the other trapped group members or nestlings. My findings suggest that many offspring delayed dispersal to form family groups, but few in Texas delay dispersal into adulthood. This suggests that young hawks obtain fitness benefits, either by benefitting from philopatry or avoiding costs associated with dispersal, prior to their second prebasic molt and then either disperse to obtain independent reproduction or to join another breeding group as a subordinate auxiliary. The timing patterns of delayed dispersal in south Texas Harris's hawks indicates that prolonged parent-offspring associations may provide cooperative benefits post-fledging, but I found little evidence that these benefits are sufficient to maintain groups

formed through natal philopatry beyond the first year of the individual's life.

I emphasize that my study is the lowest possible estimate of delayed dispersal. It is very likely that some banded fledglings were missed during censuses, despite being present in the territory. I only successfully located four of the banded nestlings outside their natal territories and only disperser was documented to join another social group. When a banded offspring disappeared from their natal territory, I could not distinguish between dispersal and mortality, which could be addressed by future researchers interested in dispersal patterns for cooperative breeders using telemetry to track fledglings once their leave their natal territories.

Delayed dispersal in Harris's hawks revealed sex-biased patterns of philopatry, with males more likely to remain in their natal groups and delaying their dispersal longer than females. One possible explanation for the differences in male versus female philopatry for Harris's hawk fledglings is increased local mate competition (Perrin and Mazalov 2000). Male-biased natal philopatry patterns were consistent with observations of competition for mates among male Harris's hawks, specifically, sex-biased natal philopatry is predicted for the sex that suffers from the most limited opportunities to breed (Komdeur et al. 2017). Census observations of group membership found 80% of adult auxiliary group members were males (*n* = 12), supporting the conclusion that breeding opportunities were less available to males than females.

Fledglings in territories occupied by breeding pairs remain philopatric more often and for longer than those in group-occupied territories, but these differences were not significant. This suggests that potential conflicts or beneficial interactions between mature auxiliary group members and delayed dispersing offspring are not significantly impacting the occurrence or

length of natal philopatry. Similarly, the presence of related juvenile auxiliaries, primarily delayed dispersers, did not impact reproductive output or philopatry which provides no evidence that Harris's hawk groups increase their fitness through collective action when offspring remain philopatric. This suggests that natal philopatry might function as extended parental investments (Ekman et al. 2001a, Kokko and Ekman 2002), in which offspring acquire skills, avoid dispersal-related mortality, and obtain other social benefits prior to seeking independent breeding opportunities (Stacey and Ligon 1991).

Conspecific density, measured as the inverse of nearest neighbor distance (NND), increased the occurrence of delayed dispersal in Harris's hawks (Figure 2), but the trend was border-line insignificant. This suggests that ecological constraints may restrict dispersal due to a shortage of breeding opportunities as conspecific density increases. Previous work in New Mexico attempted to determine the environmental covariates of breeding habitat selection and group formation (Bednarz and Ligon 1988). These results indicated breeding territories were available for occupancy, but predominately male auxiliaries remained philopatric in their natal groups, again supporting mate access as the primary constraint. Alternatively, increased conspecific density could reflect high quality territories, which incentivize natal philopatry by increasing access to resources or potential territory inheritance (Stacey and Ligon 1991, Ekman et al. 2001b).

The documentation of extra-pair reproduction in Harris's hawks confirms previous speculation that copulations between breeding hawks and auxiliaries leads to mixed parentage in some broods (Mader 1975). Extra-pair copulations between breeders and mature auxiliaries were observed 13 times in five different territories; four were polyandrous and one was

polygynous. Lack of parental genotypes and low levels of polymorphism among genotyped loci made distinction between full siblings and half siblings inconclusive at 54% of the sampled nests, but at the 17 nests where I was able to classify likely parentage; 58% were monogamous, cooperative polygamy was suspected in 24% of broods, and 18% were confirmed to contain extra-pair nestlings. This suggests some mature auxiliaries obtain a portion of reproduction and could help explain how Harris's hawks balance the cost of forming cooperative groups instead of attempting to breed independently and is the first time this strategy has been confirmed for Harris's hawks.

The relatedness analysis of my study population found two of the adult auxiliaries sampled (*n* = 5) were related to the nestlings and multiple parentage (more than two parents) was confirmed at three of 37 sampled nests (Figure 5). Adult auxiliary group members who joined their natal groups through delayed dispersal could increase their likelihood of mating with close relatives (Greenwood 1980), particularly in long-lived species like Harris's hawks. Inbreeding avoidance may therefore favor dispersal once an individual reaches sexual maturity in species who engage in extra-pair copulations (Riehl 2013, Komdeur et al. 2017). My findings suggest that auxiliary adults in nesting territories in Texas are unlikely to be offspring from previous years. I suggest that young, philopatric hawks gain cooperative benefits, such as nepotic treatment from parents (Ekman and Griesser 2002) or increased prey biomass from cooperative hunting (Bednarz 1988), in their natal groups until a breeding opportunity becomes available. Individuals may accept subordinate positions as non-kin auxiliaries outside their natal territory as long as the cooperative benefits of immigration to a non-kin group, like access to extra-pair copulations or higher quality territories, outweigh the benefits of group membership

in the individual's natal territory or of attempting to breeding independently (Seddon et al. 2005, Riehl 2013).

The formation of Harris's hawk social groups through natal philopatry is consistent with primarily RD benefits because: (1) the presence of juvenile auxiliaries did not impact any measure of reproductive output, (2) natal philopatry increased as population density increased, (3) sex-biased philopatry, for males, was consistent for the sex with the most limited breeding opportunities, (4) long-term stability of social associations between delayed dispersers and their parents is low, (5) delayed dispersal was not influenced by the presence of adult auxiliaries, and (6) natal philopatry was not influenced by annual variation or habitat urbanization.

CA benefits still may be the dominant driver of cooperative associations between adult group members that form independent of delayed dispersal. Harris's hawk reproductive output was reduced under drought conditions, but positively impacted by habitat urbanization. These findings suggest mature hawks more likely form cooperative groups due to CA benefits in undeveloped habitats, which may be highly susceptible to environmental instability. Those benefits could include social foraging (Ellis et al. 1993), increased provisioning of offspring (Dawson and Mannan 1991a), improved body condition at fledging (Bolopo et al. 2019), increased hunting success in complex or challenging habitats (Stander 1991, Hayward et al. 2006, Coulson and Coulson 2013), offspring defense (Pusey and Packer 1994), or to buffer survival against environmental instability (Covas et al. 2008, Shen et al. 2016).

During the winter months in New Mexico, Harris's hawks obtained CA benefits when individuals formed cooperative hunting coalitions that increased the energy intake per

individual compared to small hunting parties (Bednarz 1988). Cooperative hunting behavior was common and not constrained to the breeding season in my study area in Texas. Hunting parties grouped together on elevated perches to scan for prey. When a target prey was located, different group members would drop from their perches into the brush after the prey, sometimes resuming the hunt on foot. Direct hunting observations were difficult because of thick vegetation and limited visibility in south Texas, but I observed several successful cooperative hunts where group members shared the spoil (n = 7). During the winter months, I occasionally observed large groups (5+) that included multiple sex and age classes, individuals from adjacent territories, and hawks of unknown origin. I did not observe any successful hunts from these mixed-group aggregations but did successfully capture individuals from separate social-groups simultaneously on three separate occasions, once on the same Bal-Chatri trap. I suggest possible that cooperative hunting may be the primary promotor of sociality and other fitness or reproductive advantages could be a secondary benefit, but the link between social foraging and cooperative breeding remains to unclear in Harris's hawks and most cooperatively hunting species.

In sum, patterns of natal philopatry among Harris's hawk fledglings follow predictions for sex-biased delayed dispersal due to ecological constraints, specifically males may have limited access to reproductively available females. Natal philopatry that results from increased local competition is a RD benefit because it increases the fledgling's access to critical resources but decreases the per-capita available resources among all group members (i.e., critical resources are limited and unaffected by group size). Social group formation in adult Harris's hawks was suspected to be largely independent of natal philopatry, suggesting that the factors

that encourage sociality among adults could be ecologically distinct from those that influence delayed dispersal patterns. Socially breeding groups were more likely to be found in habitats with low anthropogenic influence, which suggests either 1) undeveloped habitats require more than a breeding pair to reproduce successfully or 2) the benefits of social group formation increase in undeveloped habitats significantly enough to justify foregoing or sharing reproduction with other group members. In both cases, the dual benefits framework predicts the benefits obtained by cooperation among adult Harris's hawks are collective action benefits because the benefits are the direct result of cooperative interactions among group members. My findings highlight key differences in the ecological drivers of group formation between philopatric offspring and mature auxiliaries, although it is important to note that there is likely overlap in the factors that promote RD and CA benefits. For example, juvenile auxiliaries may increase cooperative hunting success significantly, which provides a CA benefit to the group, while still primarily remaining philopatric because of ecological constraints.

Future work on Harris's hawks should expand upon my findings with the dual benefits framework. Importantly, cooperative hunting has been shown in other populations of Harris's hawks to play a significant role in provisioning the social group during the non-breeding season (Bednarz 1988), but how it interacts with cooperative group formation, stability, and breeding strategy has not been assessed. I propose the next phase of research should focus on how sociality influences hunting patterns during the breeding and non-breeding season and on measuring spatial and temporal variation in habitat quality, specifically prey resources and anthropogenic development. Teasing apart the impacts of urbanization on habitat quality and prey availability could clarify how Harris's hawks use cooperation to optimize their performance

based upon ecological conditions and provide insight on their ability to adapt to progressively urbanized environments. Paired with techniques like VHF-telemetry, which can track focal hawks to assess hunting (Bednarz 1988), a thorough study of how habitat selection influences sociality would also be helpful in facilitating our understanding of cooperation in this unique raptor species. The success of future cooperative studies relies upon recognizing ecologically divergent forms of sociality, such as those exhibited by south Texas Harris's hawks, by using more holistic approaches that consider a variety of complex, non-mutually exclusive selective forces like nepotism and environmental variation.

Table 1: Reproductive output for Harris's hawks in south Texas by year, adult social-unit size, and habitat urbanization.

Study-wide Reproductive Output (Counts)		Nesting Territories	Nest Attempts	Successful Nests	Offspring Fledged	Second Brood[c]
Nesting Year	2018	16	16	11	20	0
	2019	36	45	37	76	5
Social-unit Size[a]	Breeding Pair	24	30	24	44	3
	Social Group	21	25	20	42	2
Habitat Urbanization	Undeveloped	24	25	19	27	0
	Urban	28	36	29	69	5
Total		41[b]	61	48	96	5

[a] Six territories were excluded from summary statistics for social-unit size. [b] 11 of the 41 censused territories were monitored in 2018 and 2019. [c] At least two successful nest attempts annually in the same territory.

Table 2: Per capita reproductive output for Harris's hawks nests and territories in south Texas. Summary statistics between reproductive output and year, adult social-unit size, and habitat urbanization.

Per Capita Reproductive Output		Nest-Level		Territory-Level	
		Brood Size	Nestlings Fledged	Annual Attempts	Annual Fledglings
Nesting Year	2018	1.8 ± 0.6	1.7 ± 0.6	1.0	1.3 ± 0.9
	2019	2.2 ± 0.9	2.1 ± 0.9	1.3 ± 0.5	2.0 ± 1.5

(table continues)

Per Capita Reproductive Output		Nest-Level		Territory-Level	
		Brood Size	Nestlings Fledged	Annual Attempts	Annual Fledglings
Social-unit Size[a]	Breeding Pair	2.1 ± 0.7	2.0 ± 0.8	1.3 ± 0.5	1.9 ± 1.5
	Social Group	2.1 ± 0.9	2.1 ± 1.0	1.2 ± 0.4	1.9 ± 1.4
Habitat Urbanization	Undeveloped	1.8 ± 0.7	1.7 ± 0.7	1.1 ± 0.3	1.3 ± 0.9
	Urban	2.3 ± 0.9	2.2 ± 0.9	1.3 ± 0.5	2.1 ± 1.7
Total		2.1 ± 0.8	2.0 ± 0.9	1.2 ± 0.5	1.9 ± 1.4

[a] Six territories were excluded from summary statistics for social-unit size.

Table 3: Estimation results for fixed effects and random effects on the occurrence of delayed dispersal by the generalized linear mixed model with binomial link function.

Predictor Variables	Effect	Lower CI (95%)	Upper CI (95%)	*p*
Nestling Sex (Male)	11.45	0.49	22.41	0.041
Nearest Neighbor Distance	-9.25	-18.81	0.31	0.058

Table 4: Demographic information of 23 auxiliary group members caught at active Harris's hawk nests in south Texas by kinship designation using r_w pairwise relatedness estimates between auxiliaries and nestlings or breeding hawks.

Age/Sex Class	Kin	Non-kin	Unknown	Total
Juvenile	15	0	1	16
Adult	2	3	2	7
Female	9	0	1	10
Male	8	3	2	13
Total	17	3	3	23

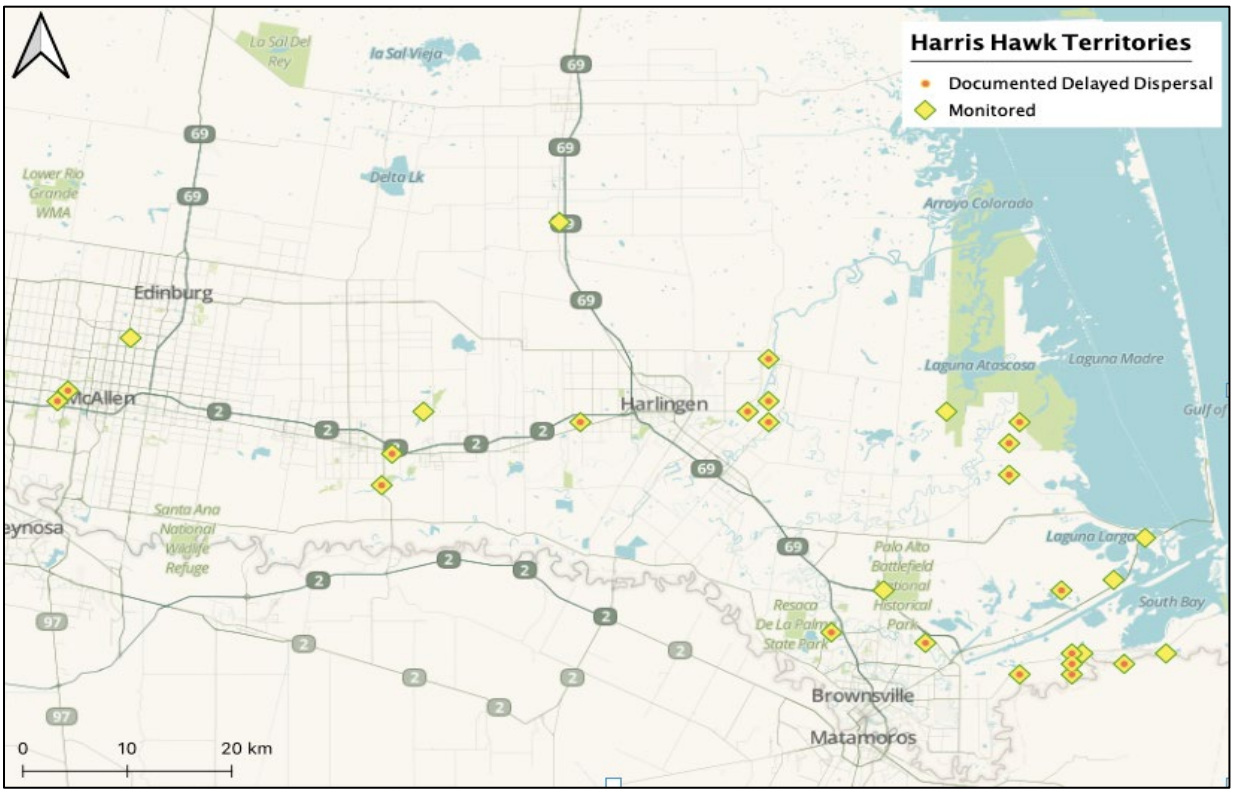

Figure 1: Occupied Harris's hawk territories that were monitored during the censuses in the lower Rio Grande Valley. All territories were monitored in spring, summer, and winter of 2018 and 2019 and in 2020 during the spring and summer.

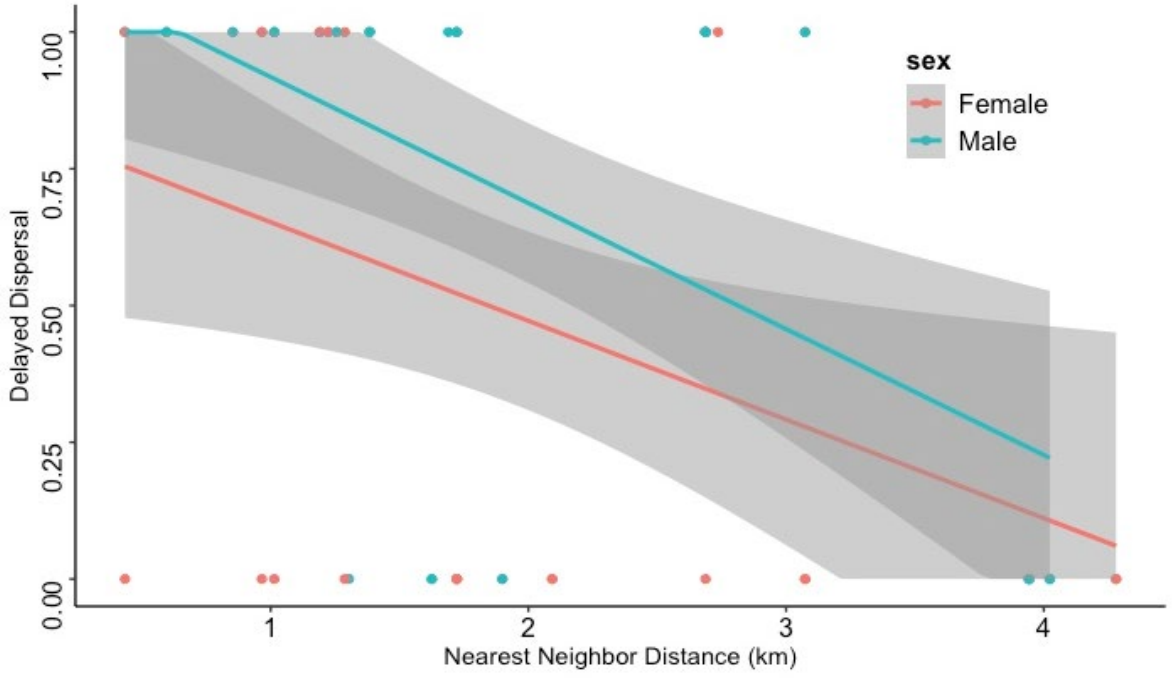

Figure 2: Sex and nearest neighbor distance influenced the occurrence of delayed dispersal in sampled nestlings at nests in Harris's hawks territories in south Texas.

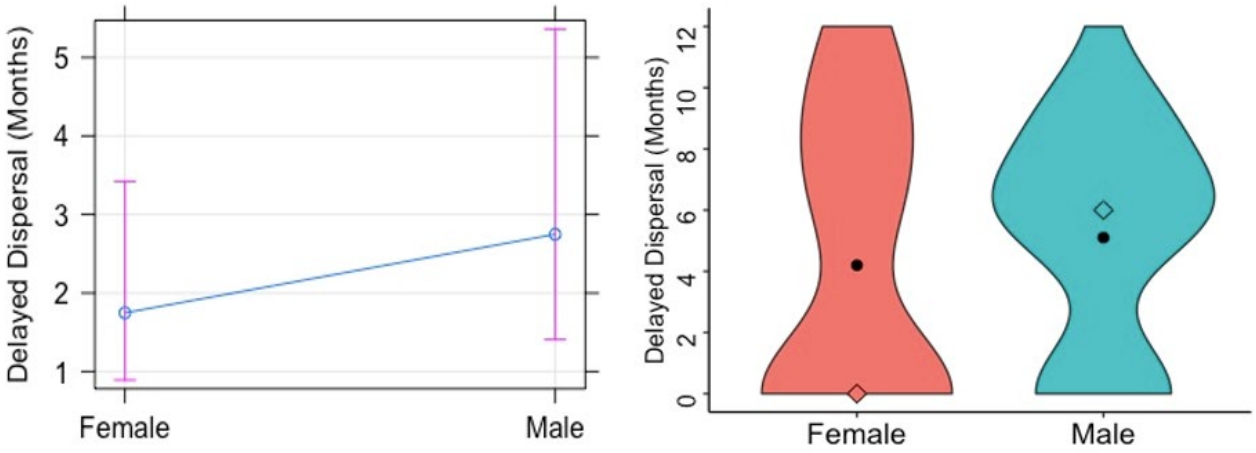

Figure 3: (Left) Sex effect from GLMM for the length of delayed dispersal in sampled nestlings at nests in Harris's hawks territories in south Texas. (Right) Length of delayed dispersal for each nestling sex with mean (filled circle) and median (unfilled diamond).

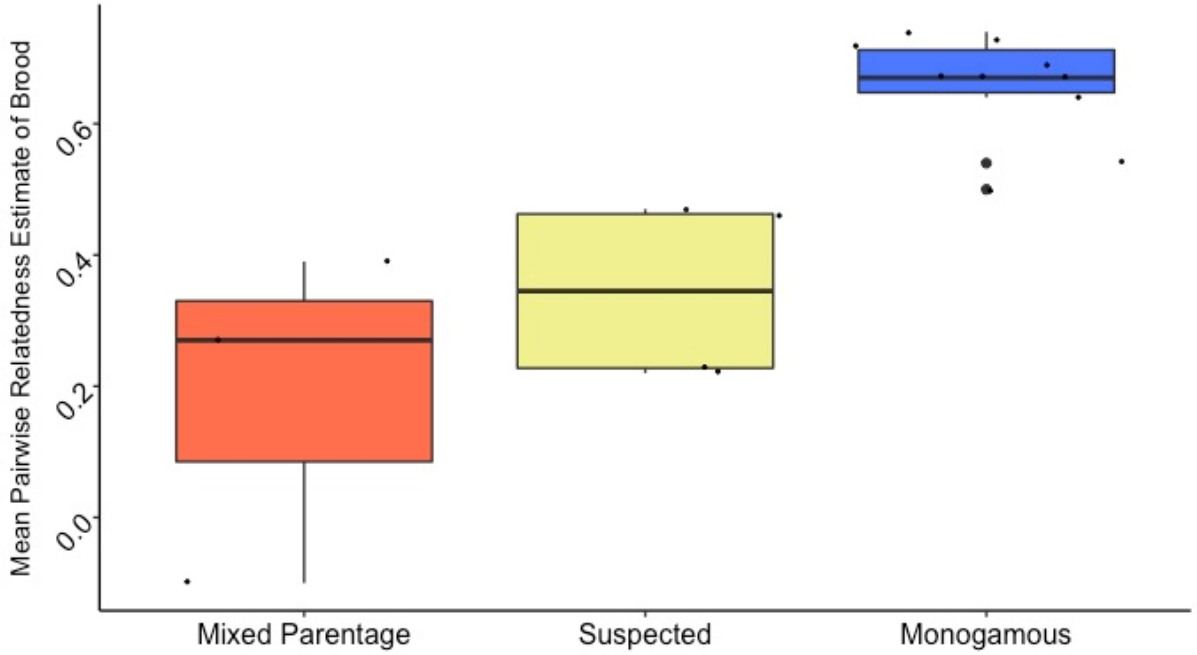

Figure 4: Parentage of 17 Harris's hawk broods in south Texas, including confirmed mixed parentage broods (*n* = 3), monogamous parentage broods (*n* = 10), and broods where mixed parentage was suspected but could not be confirmed (*n* = 4).

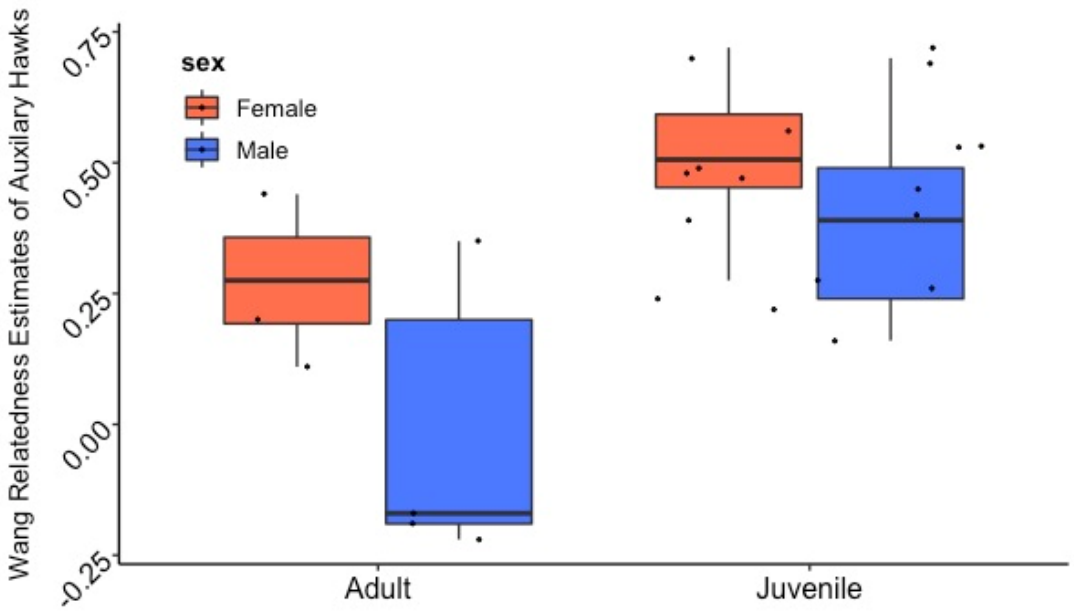

Figure 5: Average pairwise-relatedness (r_w) estimates for 23 auxiliary Harris's hawks trapped at 14 nesting territories compared with the nestlings, or a breeding adult when nestlings unavailable (see methods).

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APPENDIX:

SUPPLEMENTAL TABLES

Table A.1: Delayed dispersal and extended natal philopatry in south Texas Harris's hawk's.

Patterns of Delayed Dispersal (Natal Philopatry)		Nestlings Sampled	Delayed Dispersal[a]	Extended Philopatry[b]	Length (months)	
					Mean	Median
Nesting Year	2018	16	9	0	3.8 ± 3.5	6
	2019	49	29	5	4.9 ± 4.4	6
Nesting Sex	Males	30	21	1	5.1 ± 3.7	6
	Females	35	17	4	4.2 ± 4.7	0
Habitat Urbanization	Undeveloped	42	23	5	6.1 ± 5.0	9
	Urban	23	15	0	3.7 ± 3.5	6
Social-unit Size	Breeding Pair	36	24	3	5.1 ± 4.0	6
	Social Group	29	14	2	4.0 ± 4.5	0
Total		65	38	5	4.6 ± 4.3	6

[a] Natal philopatry for > 6 mo. [b] Natal philopatry for > 12 mo

Table A.2: Mixed parentage of 17 multi-nestlings Harris's hawk broods.

Parentage	Nest	Brood Size	Mean Nest r_w	Confirmation Method
Mixed	Boca Chica	2	-0.10	$r_w < 0.0$, Extra-pair copulations
	Bahia Grande	3	0.39	Diploid inheritance patterns
	Country Road	4	0.27	Diploid inheritance patterns
Suspected Mixed	Kingston	3	0.22	$r_w < 0.25$, Extra-pair copulations
	Estero Llano '19	4	0.23	$r_w < 0.25$, 1 locus mismatch
	Bayside Loop	3	0.46	1 locus mismatch
	Weslaco	3	0.47	Offspring with upper r_w CI < 0.45

(table continues)

Parentage	Nest	Brood Size	Mean Nest r_w	Confirmation Method
Monogamous	Palmito Hill	2	0.50	$r_w > 0.5$, mother genotype
	Fish Hatchery	2	0.67	$r_w > 0.5$, mother genotype
	Highway 511	2	0.73	$r_w > 0.5$, lower r_w CI > 0.20
	Zillock Ranch	2	0.54	$r_w > 0.5$, both parent genotypes
	Williams Rd	2	0.67	$r_w > 0.5$, lower r_w CI > 0.20
	Estero Llano '20	4	0.74	$r_w > 0.5$, both parent genotypes
	Palmito Road	2	0.67	$r_w > 0.5$, lower r_w CI > 0.20
	Cemetery	2	0.64	$r_w > 0.5$, lower r_w CI > 0.20
	Violet	2	0.69	$r_w > 0.5$, lower r_w CI > 0.20
	Massey	2	0.72	$r_w > 0.5$, lower r_w CI > 0.20

Table A.3: Pairwise relatedness (r_w) and 95% CI of each nestling in 17 Harris's hawk broods where broods were likely monogamous (*n* = 10), mixed parentage was confirmed (*n* = 3) or suspected (*n* = 4).

Confirmed Mixed Parentage					
Nest	**Extra-Pair Nestling**	**Nestling 2**	**Nestling 3**	**Nestling 4**	**Parent(s)?**
Boca Chica	-0.10 (-0.28, 0.09)	-0.10 (-0.28, 0.09)	N/A	N/A	No
Bahia Grande	0.18 (-0.12, 0.63)	0.18 (-0.12, 0.63)	0.62 (0.29, 0.92)	N/A	No
	0.38 (0.00, 0.64)	0.62 (0.29, 0.92	0.38 (0.00, 0.64)		
Country Road	0.24 (-0.07, 0.74)	0.18 (-0.12, 0.43)	0.35 (-0.03, 0.76)	0.24 (-0.07, 0.74)	No
	0.18 (-0.12, 0.43)	0.41 (0.05, 0.81)	0.18 (-0.16, 0.65)	0.41 (0.05, 0.81)	
	0.35 (-0.03, 0.76)	0.25 (-0.07, 0.77)	0.25 (-0.07, 0.77)	0.18 (-0.16, 0.65)	

(table continues)

Suspected Mixed Parentage					
Nest	**Extra-Pair Nestling**	**Nestling 2**	**Nestling 3**	**Nestling 4**	**Parent(s)?**
Kingston	0.10 (-0.22, 0.48)	0.16 (-0.18, 0.55)	0.10 (-0.22, 0.48)	N/A	No
	0.16 (-0.18, 0.55)	0.40 (0.00, 0.80)	0.40 (0.00, 0.80)		
Bayside Loop	0.27 (0.01, 0.59)	0.39 (0.12, 0.55)	0.72 (0.47, 0.96)	N/A	No
	0.39 (0.12, 0.55)	0.72 (0.47, 0.96)	0.27 (0.01, 0.59)		
Weslaco	0.35 (0.08, 0.46)	0.80 (0.46, 1.00)	0.28 (-0.10, 0.45)	N/A	No
	0.28 (-0.10, 0.45)	0.35 (0.08, 0.46)	0.80 (0.46, 1.00)		
Estero Llano Grande State Park 2019	0.02 (-0.19, 0.35)	0.17 (-0.31, 0.68)	0.02 (-0.19, 0.35)	0.39 (0.18, 0.70)	Both
	0.12 (-0.19, 0.43)	0.12 (-0.19, 0.43)	0.39 (0.18, 0.70)	0.53 (0.18, 0.70)	
	0.31 (0.02, 0.56)	0.53 (0.18, 0.70)	0.17 (-0.31, 0.68)	0.31 (0.02, 0.56)	
Suspected Monogamous Broods					
Nest	**Nestling 1**	**Nestling 2**	**Nestling 3**	**Nestling 4**	**Parent(s)?**
Palmito Hills	0.50 (0.20, 0.73)	0.50 (0.20, 0.73)			Female
Fish Hatchery	0.67 (0.23, 0.93)	0.67 (0.23, 0.93)			Female
Highway 511	0.73 (0.28, 0.93)	0.73 (0.28, 0.93)			No
Zillock Ranch	0.54 (0.30, 0.76)	0.54 (0.30, 0.76)			Both
Williams	0.67 (0.38, 0.93)	0.67 (0.38, 0.93)			No
Palmito Road	0.67 (0.42, 0.88)	0.67 (0.42, 0.88)			No
Cemetery	0.64 (0.42, 0.82)	0.64 (0.42, 0.82)			No
Violet	0.69 (0.46, 0.91)	0.69 (0.46, 0.91)			No
Massey	0.72 (0.60, 0.94)	0.72 (0.60, 0.94)			No

(table continues)

Nest	Nestling 1	Nestling 2	Nestling 3	Nestling 4	Parent(s)?
Estero Llano Grande State Park 2020	0.33 (0.21, 0.70)	0.33 (0.21, 0.70	0.66 (0.28, 0.87)	0.79 (0.32, 0.97)	Both
	0.66 (0.28, 0.87)	0.57 (0.31, 0.84)	0.57 (0.31, 0.84)	0.66 (0.28, 0.87)	
	0.78 (0.62, 0.97)	0.50 (0.23, 0.78)	0.79 (0.32, 0.97)	0.78 (0.62, 0.97)	

Table A.4: Relatedness (pairwise r_w, 95% CI) and corresponding kinship designation of 23 auxiliary group members at Harris's hawk territories in the lower Rio Grande Valley of south Texas.

Age	Sex	Relatedness to Territory Nestlings or Breeding Pair				Kinship Designation
		Individual 1	Individual 2	Individual 3	Mean	
Adult	Female	0.44 (0.04, 0.83)			0.44	Kin[a]
Adult	Male	-0.22 (-0.40, 0.06)			-0.22	Non-kin
Juvenile	Female	0.28 (-0.06, 0.70)			0.28	Kin
Juvenile	Female	0.53 (0.30, 0.46)			0.53	Kin
Juvenile	Female	0.35 (0.07, 0.65)			0.35	Kin
Juvenile	Male	0.39 (0.03, 0.74)			0.39	Kin
Juvenile	Male	0.45 (0.39, 0.63)			0.45	Kin
Juvenile	Male	0.25 (0.06, 0.60)			0.25	Kin
Adult	Male	0.41 (0.04, 0.78)	0.28 (0.02, 0.52)		0.21	Kin
Juvenile	Male	0.79 (0.03, 0.95)	0.61 (0.43, 0.82)		0.70	Kin
Juvenile	Male	0.52 (0.20, 0.72)	0.54 (-0.10, 1.00)		0.53	Kin
Juvenile	Male	0.52 (0.40, 0.64)	0.47 (0.38, 0.58)		0.50	Kin
Juvenile	Female	0.61 (0.47, 0.85)	0.76 (0.43, 0.93)		0.69	Kin
Juvenile	Female	0.91 (0.74, 1.00)	0.53 (0.13, 0.86)		0.72	Kin
Juvenile	Female	0.44 (0.01, 0.85)	0.51 (0.25, 0.84)		0.48	Kin

(table continues)

Age	Sex	Relatedness to Territory Nestlings or Breeding Pair				Kinship Designation
		Individual 1	Individual 2	Individual 3	Mean	
Juvenile	Female	0.66 (0.32, 0.92)	0.46 (-0.09, 0.75)		0.56	Kin
Juvenile	Male	0.42 (0.05, 0.60)	0.07 (-0.31, 0.33)		0.25	Kin
Adult	Male	0.24 (-0.02, 0.41)	0.17 (-0.08, 0.47)		0.21	Unknown
Juvenile	Male	0.21 (-0.33, 0.67)	0.11 (-0.33, 0.50)		0.16	Unknown
Adult	Female	0.04 (-0.17, 0.33)	0.18 (-0.27, 0.65)		0.11	Unknown
Adult	Male	-0.18 (-0.37, 0.05)	-0.09 (-0.40, 0.21)	-0.23 (-0.64, 0.05)	-0.17	Non-kin
Adult	Male	-0.1 (-0.25, 0.13)	-0.09 (-0.42, 0.13)	-0.38 (-0.57, -0.27)	-0.19	Non-kin
Juvenile	Female	0.63 (0.42, 0.82)	0.39 (0.00, 0.73)	0.40 (-0.09, 0.74)	0.47	Kin